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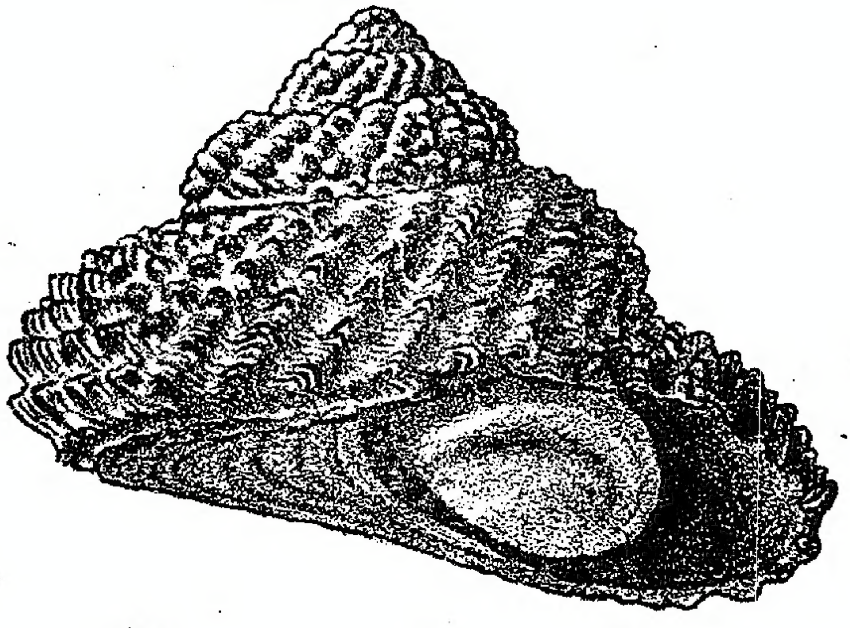

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NEW ZEALAND CHITONS

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Chitons are the molluscs with limpet-like shapes and habits, but with a shell made up of eight separate, partly overlapping pieces called valves. They are placed in a class of molluscs on their own, called Polyplacophora. Most chitons are grazing herbivores, living under boulders in the intertidal zone or in shallow subtidal depths, a few occur in the open in the higher intertidal and a few occur in the deep sea. We have quite a large fauna of them in New Zealand (48 species and subspecies recognised here) and many species are highly variable and occupy a range of ecological niches. In their major monograph of New Zealand chitons, Iredale and Hull (1929-32) recognised many minor ecological variants as species and used a large number of genera, but anyone reading literature on American and European chitons will soon realise that many of our species are very similar to South American and Northern Hemisphere ones, and belong in world-wide genera that were used here by Suter but not by later workers. Since Iredale and Hull (1929-32), many papers affecting the names of our chitons have been published by Eugene Leloup, in Brussells (see bibliography, where only some of them are listed). The writer has tried to take account of the ecological variation of our chitons, the fact that many Iredale and Hull "genera" are clearly synonyms of widespread overseas genera, and the changes proposed by Leloup, and attempted to produce a biologically realistic classification of New Zealand Polyplacophora.

Names for parts of chitons

To understand descriptions of differences between chitons, you will need to know some of the terms used for parts of the chiton shell and girdle. The following diagrams show you some of the main features of a typical chiton (based on Rhyssoplax canaliculata); the upper diagram (A) shows the top view of a whole chiton, in living position, and the lower set of diagrams (B) shows the dorsal (left) and left lateral (right) views of the anterior, intermediate, and posterior valves of the same chiton, as seen when freed from the girdle.

Girdle coverings

While the girdle of some chitons is smooth and tough, like leather, in most it is covered with various kinds of protective features. In more than half of New Zealand chitons the girdle is covered with closely spaced, overlapping, rounded, calcareous scales, superficially resembling a snake's skin. (Families Lepidopleuridae, Ischnochitonidae, Callochitonidae, Schizochitonidae, Chitonidae). In Callochitonidae these are smaller than usual, quite glassy and transparent, and can be seen to be closely appressed, oblique, tall and narrow, and resembling short, oblique, closely spaced bristles as much as tall, overlapping scales. In some chitons (Eudoxochiton and most Mopaliidae) there are flexible, chitinous bristles scattered over the girdle, or (in many Mopaliidae) arranged in dense tufts at the sides of the overlap areas of each pair of valves (called "sutural tufts"). In Acanthochitonidae the similar sutural tufts are made up of stiff calcareous spines, and the rest of the girdle may be smooth or clothed in stiff calcareous spicules. The velvet-like surface of the girdle of Onithochiton (Fam. Chitonidae) is covered with minute, closely spaced, sharply pointed, strongly ridged scales.

Shell sculpture

Most chitons have clearly distinguishable lateral and central (or pleural) areas on the exposed surface of each half of each valve, with radial ribs or rows of nodules on the lateral areas and on the end valves, and longitudinal ribs or rows of nodules on the central areas (Families Ischnochitonidae, Callochitonidae, Schizochitonidae, Chitonidae, some species in Lepidopleuridae and Mopaliidae).

In many Lepidopleuridae the sculpture consists of simple, closely spaced, small, rounded nodules all over the surface, sometimes weakly arranged in rows, but in other species not in rows, so the central and lateral areas are not always recognisable. Lepidopleuridae are also recognisable by their small size, and by lacking insertion plates (see diagrams) around the edges of valves, although they have sutural laminae between valves.

In Acanthochitonidae, lateral areas and central areas are sculptured similarly, with radial rows of low, flat, closely spaced nodules, so the two kinds of areas are usually not separable, or are separated by a low ridge only, and they are called just the lateral area only. Acanthochitonidae are recognisable also by having only 5 slits in the anterior valve, and only 5 radial ribs on the surface of the valve (if any ribs at all).

Now we can look at the features of each genus and species.

Species of N.Z. (excluding Macquarie I.) chitons

Class Polyplacophora
Order Neoloricata
Suborder Lepidopleurina
Family Lepidopleuridae Pilsbry, 1893

Small chitons with sutural laminae between the valves, but no insertion plates around the edges of the valves. Girdle with scales.

Genus Lepidopleurus Risso, 1826
Type species: Chiton cajetanus Poli, 1791, Recent, Mediterranean
Synonym: Terenochiton Iredale, 1914 (Type species: Lepidopleurus (Terenochiton) subtropicalis Iredale, 1914, Kermadec Islands).

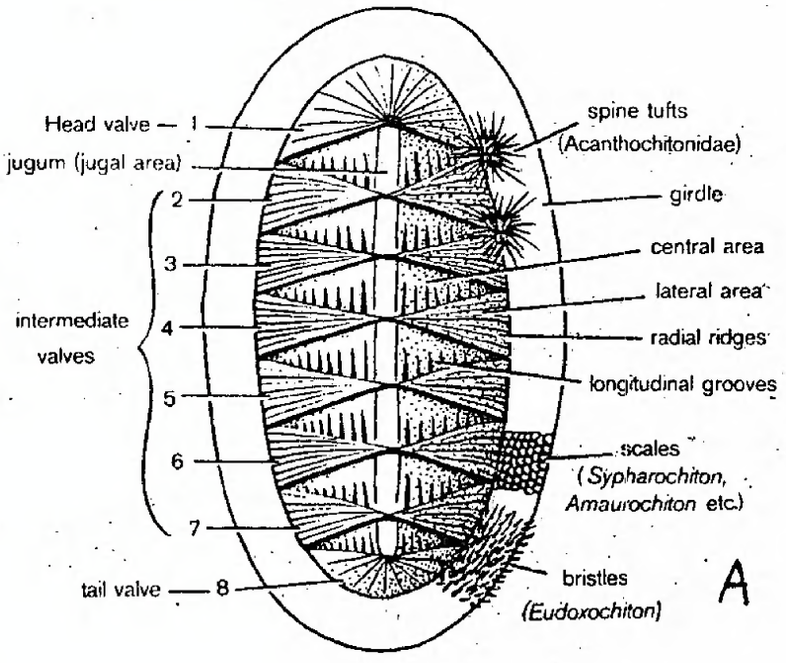
A world-wide genus of small chitons with rounded or lightly angled backs, granular sculpture, and strong transverse ridges on the small girdle scales. Tail valve short, with mucro at centre or further forward than centre.

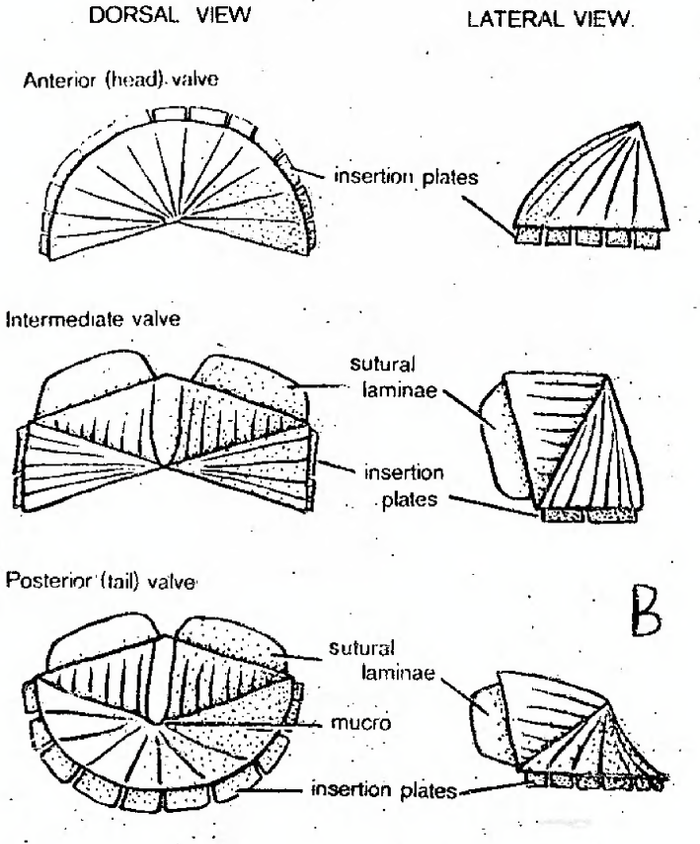
Lepidopleurus finlayi Ashby, 1929-

A very small species, not over 10mm long, with widely spaced rows of small granules, clearly arranged in radial and longitudinal rows, and with a row of peg-like spines hanging out from the posterior edge of each valve. Dredged uncommonly, from subtidal (Stewart I.) to quite deep water all around N.Z.

Lepidopleurus inquinatus (Reeve, 1847) -

Moderately large for family (to ca. 20mm), with rounded back, with closely spaced, very fine granules not clearly arranged in rows, no posterior row of spines, and often two brown spots near the centre of each valve. Intertidal (often in black mud under boulders) and continental shelf, all around N.Z.


Head valve — 1
jugum (jugal area)
2
3
intermediate valves
4
5
6
7
tail valve — 8
spine tufts (Acanthochitonidae)
girdle
central area
lateral area
radial ridges
longitudinal grooves
scales (Sypharochiton, Amaurochiton etc.)
bristles (Eudoxochiton)
A


DORSAL VIEW
LATERAL VIEW
Anterior (head) valve
insertion plates
Intermediate valve
sutural laminae
insertion plates
Posterior (tail) valve
sutural laminae
mucro
insertion plates
B

Lepidopleurus otagoensis (Iredale & Hull, 1929) -

A small (to 10 mm) species with coarser granules than in L. finlayi and L. inquinatus, lightly angled back as in L. finlayi, granules relatively closely spaced and clearly arranged in rows, no posterior spines along valve edge. Intertidal and subtidal on the shelf, Otago to Stewart I.

Lepidopleurus subantarcticus (Iredale & Hull, 1930) -

A small (to ca. 12mm) species abundant in deepwater dredgings off Otago, on Bryozoa etc., south to the N.Z. subantarctic islands. Back very steeply angled, granules coarse but evenly spaced and not clearly arranged in rows; placed in Parachiton by earlier workers, but the short tail valve is typical of Lepidopleurus.

Two probable unnamed species are known from a few valves each, from the continental shelf off the Poor Knights Islands and off Spirits Bay.

Genus Parachiton Thiele, 1909
Type species: Lepidopleurus (Parachiton) acuminatus Thiele, 1909, Duke of York Islands (Neu Lauenberg), Bismark Archipelago.

Differs from Lepidopleurus in its long tail valve, with mucro near the posterior end.

Parachiton textilis Powell, 1937 -

A rare species, described from valves from deep water off the Three Kings Islands; the single known complete shell (National Museum) is about 25mm long and 7mm wide, marbled white and pale pinkish grey, and with a long, typical Parachiton tail valve.

Family Hanleyidae Bergenhayn, 1955

n. gen., n. sp. - a minute (to ca. 4mm long) unnamed pink chiton which lives in burrows it hollows out in the calcareous crust on Cookia shells; found at Kaikoura; to be named by I. Mannering.

Suborder Ischnochitonina
Family Ischnochitonidae Dall, 1889
Genus Ischnochiton Gray, 1847
Type species: Chiton textilis Gray, 1828, South Africa

Many previous workers have followed Gray's original description of Ischnochiton textilis and believed it to have only one slit in the sides of intermediate valves. Pilsbry (1893) in his monograph of the chitons proposed the subgenus Radsiella for species with two or more slits. However, van Belle (1974) showed that Ischnochiton textilis has more than one slit, so Radsiella is a synonym of Ischnochiton, and he proposed the subgenus Simplischnochiton for species with only one slit.

Long, narrow chitons with scaly girdles and thin, sharp insertion plates. Girdle scales smooth or with transverse ridges.

Subgenus Simplischnochiton van Belle, 1974
Type species: Ischnochiton maorianus Iredale, 1914, New Zealand

Ischnochiton (Simplischnochiton) circumvallatus (Reeve, 1847) -

Usually small, but up to 40mm long, uniform coloured, usually pale in colour but can be dark tan-brown; finely sculptured, with a longer tail valve than in I. maorianus. Common from Otago south to the subantarctic islands, intertidal and dredged in shallow water.

Ischnochiton (Simplischnochiton) maorianus Iredale, 1914 -

The abundant, rapidly creeping, elongate, brightly coloured, highly variably coloured chiton, found under boulders (usually in contact with black mud), throughout mainland New Zealand. Usually much larger than I. circumvallatus, with more obvious sculpture, much brighter and more varied colour, and the tail valve not as long as in I. circumvallatus.

New genus: small Ischnochitonidae with girdle scales bearing closely spaced, stalked spheres.

(N. gen.) granulifer (Thiele, 1909) -

Small chitons, up to ca. 10mm long, with more tapered ends than young Ischnochiton maorianus of the same size, and with a surface sculpture of regularly spaced, indistinct dimples, colour marbled cream or pale pink and white, many with black or brown spots; common in shallow-water dredgings throughout mainland N.Z.

(N. gen.) luteoroseus (Suter, 1907) -

Very similar to (N. gen.) granulifer, but more parallel-sided, and with a colour pattern of much more brilliant, magenta and yellow streaks, in the same sort of pattern as in (N. gen.) granulifer - just a geographic subspecies? - shallow dredgings around N.Z. subantarctic islands.

Genus Lepidozona Pilsbry, 1892
Type species: Chiton mertensii Middendorf, 1846, western North America.

With better defined, crisper sculpture than in Ischnochiton, shorter and wider, with a more clearly defined jugal angle, and a short, toothed plate across the sinus between the sutural laminae.

Lepidozona n.sp.

Dredged uncommonly in more than 200m of water all around North Island, from Cook Strait to the Three Kings, a small species (rarely over 15mm), mainly cream, mottled grey and red on both shell and girdle, with very fine, crisp sculpture. Considerably shorter, wider, and more angled along the back than N.Z. Ischnochiton species, more resembling Rhyssoplax.

Family Callochitonidae Plate, 1899

With much more numerous slits in the edges of the insertion plates (especially of intermediate valves) than other chitons; girdle covered with characteristic glassy, dense, overlapping, inclined scales (could also be called short, dense, even-topped spicules).

Genus Callochiton Grey, 1847
Type species: Chiton laevis Montagu, 1803, Europe.
Synonyms: Icoplax Iredale & Hull, Paricoplax Iredale & Hull.

Shell relatively small (to ca. 30mm long), smooth or with deep longitudinal grooves in central areas, green, grey or (more usually) red; girdle with glassy scales only.

Callochiton crocinus (Reeve, 1847) -

An uncommon intertidal species found throughout mainland N.Z., back low and colour dark brown-red, so blends in well with rocks; shell always smooth. The name is based on Australian specimens, and N.Z. ones have never been critically compared.

Callochiton empleurus (Hutton, 1872) -

An uncommon, dredged, subtidal or (rarely) intertidal, highly variable species, grey, red or light green, highly variable in sculpture from smooth on all valves, through small grooves on central areas of some valves and not on others, to specimens with deep, wide grooves (i.e. high, thin ribs) over all central areas. Specimens with high, thin ribs all over have been called Kapitiensis Mestayer; those with a few weak grooves (the most common form) empleurus Hutton and subeudoxus Iredale & Hull; from the fiords, juveniles with a hooked mucro on each valve have been called C. sulculatus Suter (but adults in the same area are typical C. empleurus); and from subantarctic islands, those with a few weak grooves on some valves but not on others have been called C. mortenseni Odhner; I think it very likely they are part of the variation of a single species, but the narrow-ribbed, grey ones (C. kapitiensis) could be a distinct species.

(C. puniceus Gould, listed by Iredale & Hull and later workers from New Zealand, is a South American species; Dell 1971, p. 217).

Genus Eudoxochiton Shuttleworth, 1853
Type species: Chiton nobilis Gray, 1843, New Zealand.

Much larger than Callochiton, dark brown, with many horny bristles on the girdle as well as the glassy scales.

Eudoxochiton nobilis (Gray, 1843) -

Our largest chiton, to ca. 150mm long, reasonably common intertidally throughout N.Z. Quite variable in the height of the back and strength of the angle down the back, and the low-backed ones (E. huttoni Pilsbry) have the same girdle spicules, etc., as high backed ones (Leloup 1957). The valves are smooth (when not encrusted), except for a low rib between lateral and central areas.

Family Schizochitonidae Dall, 1889
Genus Lorica H. & A. Adams, 1852
Type species: Chiton cimolius Reeve, 1847, S.E. Australia.
Synonym: Aulacochiton Shuttleworth, 1853, type species Chiton volvox Reeve, 1847, S.E. Australia.

Easily recognised by the high, narrow, spiny ribs on lateral areas and on the anterior valve, by the high, narrow longitudinal ribs on central areas, by the steep, concave silhouette of the anterior valve, and by the almost terminal mucro on the very small posterior valve. Girdle with scales.

Lorica haurakiensis Mestayer, 1921 -

Quite a large chiton, usually about 30 to 60mm long, easily recognised by its bright red and cream colour, by its two or three high, narrow, widely spaced, spiny ribs on lateral areas, and the many similar ribs around the high, concave anterior valve. Intertidal and dredged in shallow water throughout New Zealand, but uncommon in most places.

Genus Loricella Pilsbry, 1893
Type species: Lorica angasi H. Adams, 1864, S.E. Australia

Similar to Lorica in appearance but with weaker sculpture, a much larger anterior valve, girdle wider anteriorly than it is posteriorly, and girdle slit to the shell in the middle of the posterior.

Loricella profundior (Dell, 1956) -

A small species, to ca. 20mm long, rarely dredged in deep water all around N.Z., with a very large anterior valve, very weak sculpture, and mottled orange and cream colouration.

Family Mopaliidae

With only minor modifications, this classification follows Leloup's (1942) monograph of world Mopaliidae, in which Iredale & Hull's "genera" are rearranged to express similarities in a much more meaningful way than Iredale & Hull (1929-32) were able to. Leloup points out the major specific characters of the girdle bristles.

Small to large chitons with the central and lateral areas separated by a radial rib only in most species, and similar wavy or zig-zag sculpture continuous over both areas of most species; eight slits and eight radial ribs in head valve (or multiples thereof, in a few genera); eight slits in tail valve (Mopalia and allies) or tail valve callused and unslit (Plaxiphora and allies); girdle leathery, with rows of horny bristles (many with calcareous tips), usually including sutural tufts of bristles similar to the calcareous spine tufts of Acanthochitonidae.

Genus Plaxiphora Gray, 1847
Type species: Chiton carmichaelis Gray, 1828 (= C. auratus Spalowsky, 1795), circum-subantarctic.
Synonyms: Macrichiton Iredale, 1914; Diaphoraplax Iredale, 1914; Poneroplax Iredale, 1914; Kopionella Ashby, 1919.

Sculpture of wavy or zig-zag ribs (becoming obsolete in adult P. aurata), and radial ribs on lateral areas and head valve; 8 slits and 8 radial ribs on anterior valve; posterior valve callused and unslit, mucro at posterior end.

Subgenus Plaxiphora sensu stricto

Plaxiphora (Plaxiphora) aurata (Spalowsky, 1795) -

A large (to 100mm) subantarctic chiton, shell with only

radial ribs when adult, but with zig-zag sculpture all over when young; girdle bristles variable from few to dense. Mannering (1974) showed that New Zealand populations identified by Powell as P. aurata campbelli Filhol are not separable from P. aurata aurata.

Plaxiphora (Plaxiphora) biramosa (Quoy & Gaimard, 1835) -

A relatively large species, to ca. 70 mm long, with coarse, closely spaced, wavy sculpture all over, usually cream and bright green, girdle brick red, with a wide shell, and with only the sutural bristle tufts and one other narrow row of bristles on an otherwise naked girdle. Uncommon, found only on extremely exposed, wave-washed boulders, all around New Zealand.

Plaxiphora (Plaxiphora) caelata (Reeve, 1847) -

Two subspecies are recognised -

P. caelata caelata -

Shell up to ca. 40 mm long (usually smaller), highly variable in height of back, in strength of the zig-zag sculpture, and in colour. Most specimens are uniform olive green to green-black; high-backed specimens with fine sculpture and a black and white colour pattern have been called "Maorichiton" metonomazus Iredale & Hull. Smaller and narrower than P. biramosa, and girdle with many more bristles all over the girdle, as well as the sutural tufts. Reasonably common intertidally throughout mainland New Zealand. (= "Kopionella mathewsi" of Willan (1972), not of Australian workers).

P. caelata schauinslandi Thiele, 1909 -

Specimens from the Chatham Islands agree in almost all features with P. caelata, but reach a considerably larger size (up to 70 mm) and have more prominent radial ribs on the anterior valve than mainland specimens. Probably a weakly differentiated geographic subspecies.

Subgenus Guildingia Dall, 1882
Type species: Plaxiphora (Guildingia) Obtecta Pilsbry ex Carpenter MS, 1893, New Zealand

Girdle wide, valve surface relatively small and smooth; bears a similar relationship to Plaxiphora as the northern hemisphere Katherina does to Mopalia, although not as advanced along the path of girdle widening as Katherina is.

Plaxiphora (Guildingia) obtecta Pilsbry, 1893 -

A specialised Plaxiphora in which the girdle has encroached a little on the exposed valve area, so the girdle is very wide and the visible shell area relatively small. Shell surface smooth, polished, usually dark green; girdle densely bristled all over, without sutural tufts. A large species (to at least 80 mm) common in very exposed situations in northern North Island, occurring uncommonly to southern South Island.

Subgenus Fremblya H. Adams, 1866
Type species: Fremblya egregia H. Adams, 1866, New Zealand.

Shell small, short and wide, with unusually prominent sculpture.

Plaxiphora (Fremblya) egregia (H. Adams, 1866) -

The sole species of the subgenus, small (to ca. 30 mm at most), almost as wide as long, with very prominent longitudinal and radial sculpture; girdle with large sutural bristle tufts, but otherwise only a marginal fringe of bristles. Lives only under Durvillea kelp holdfasts; Wellington south coast to southern N.Z.

Subgenus Vaferichiton Iredale & Hull, 1932
Type species: Plaxiphora murdochi Suter, 1905, New Zealand

Small species (none over about 20 mm long), with very fine sculpture on the valves, or virtually no sculpture at all, and only a few sparse spicules on the finely scaled girdle.

Plaxiphora (Vaferichiton) australis Suter, 1907 -

Not more than 10 mm long, black, almost smooth, with two or three long, glassy spicules at each valve suture only. Intertidal, Snares Islands.

Plaxiphora (Vaferichiton) murdochi Suter, 1905 -

Larger than australis (ca. 20 mm), low and broad, with sculpture of exceedingly fine, close, wavy sculpture all over shell; dull olive green, with longitudinal to irregular bluish translucent lines. Girdle reddish brown, narrow, with sparse, irregularly placed, horny bristles. Below lowest tide mark, beneath large, smooth, extremely exposed boulders on exposed shores of west coast from Auckland to Westland.

Plaxiphora (Vaferichiton) new species -

Two unnamed species are known to date, and probably more will be discovered: one from Wellington south coast to E. Otago is small, black, like australis but with dimpled shell sculpture, and no sutural bristle tufts; the other is known from Kaikoura to the subantarctic islands, is larger (to 15 mm or more), flattened, dark reddish brown (to be named by I. Mannering).

Genus Placiphorella Dall, 1879
Type species: Placiphorella velata Dall, 1879, Western North America

Valves very short and wide, so the shell area is almost circular; girdle narrow posteriorly, but extremely wide anteriorly; sculpture of obscure dimples only; anterior valve with 8 to 20 or more shallow slits in the short, very thick insertion plates. Intertidal in W. North America; also widely known in deep water (the species with multi-slit insertion plates).

Placiphorella n.sp. -

A collection of several separated valves from 500 m off the Three Kings Islands has the extremely short, wide valves and finely dimpled surface of Placiphorella, and has more than 20 slits around the very short, thick insertion plates of the anterior valve. The genus has not previously been recorded from the southern hemisphere, to my knowledge.

Family Chitonidae Rafinesque, 1815
Genus Chiton Linnaeus, 1758
Type species: Chiton tuberculatus Linnaeus, 1758, Caribbean.
Synonyms: Amaurochiton Thiele, 1909; Sypharochiton Thiele, 1909; and several "genera" proposed for Australian species by Iredale & Hull.

Large, mostly strongly sculptured chitons, with coarse girdle scales, and thick, elaborately dissected (comblike, or pectinate) teeth on the insertion plates of all valves. Mucro of posterior valve central.

The type species of Amaurochiton Thiele, C. latus Sowerby, is a very large, wide, coarsely sculptured South American species (to ca. 80 mm long) bearing little resemblance to C. glaucus from New Zealand. In fact these "genera" were proposed by Thiele (1909, 1910) as sections of Chiton on the basis of minor radular differences, and the shells of all these species are so similar they are best placed in one genus, as they have been by recent overseas workers.

Chiton glaucus Gray, 1828 -

The well known, moderately large (to ca. 40 mm), low-backed, dark olive green, finely and evenly sculptured species, abundant under intertidal boulders throughout New Zealand. Northern North Island specimens have paler radiating colour bands, and may be yellow, blue, brown, or red, as well as the dull green found elsewhere in N.Z.

Chiton pelliserpentis Quoy & Gaimard, 1835 -

The "snake's skin" chiton, extremely abundant from high to low in the intertidal zone throughout N.Z., often out in the open on rock surfaces. Sculpture of prominent, nodulose, rounded radial ribs on lateral areas and end valves, and of prominent, nodulose, longitudinal ribs on central areas; colour variable, dull to bright black and white. Specimens from low in the intertidal zone, sheltered under boulders, have bright colour, with additional narrow pale blue and red-brown lines, and have been known as sinclairi, whereas those exposed on bare rock surfaces are eroded and dull, and have been regarded as typical pelliserpentis; Boyle (1970) showed that these belong in one variable species.

Chiton torri Suter, 1907 -

An extremely small (to ca. 12 mm), black, almost smooth species, with a coarsely scaled girdle. Common at Bluff and at Stewart Island.

Genus Rhyssoplax Thiele, 1893
Type species: Chiton affinis Issel, 1869, Gulf of Suez.
Synonym: Anthochiton Thiele, 1893, Type species: Chiton tulipa Quoy & Gaimard, 1835, South Africa.

With smaller girdle scales, finer and crisper sculpture, and a more clearly keeled jugum than Chiton; jugum smooth.

Rhyssoplax canaliculata (Quoy & Gaimard, 1835) -

An extremely variable species, uncommon but occurring throughout N.Z., south to the Auckland Islands. Dredged specimens are high-backed, bright pink, often with black jugal areas, and are typical

canaliculata; intertidal northern specimens with low backs, green, red or mottled colour, and with relatively coarse sculpture, have been called aerea Reeve; from the same area, but small, finely sculptured, dappled shells, have been called stangeri Reeve; from the same area again (mainly Rangitoto Island), similar to aerea but with a few large knobs on radial ribs, have been called clavata Suter; a few low-backed, mottled green, crisply sculptured intertidal ones from eastern South Island have been identified as suteri Iredale; large, olive green, sparsely sculptured ones from the intertidal zone of Otago have been called huttoni Suter; and the few high-backed, green specimens collected with typical pink canaliculata have been called aerea. There is a complete gradation in the height of the back (the jugal angle) between intertidal and dredged specimens (as in most N.Z. chitons), a complete gradation in colour from black to white through brown, red, pink, orange, green, and all dappled combinations, and a complete gradation in sculpture from almost smooth, with a few sparse grooves, to closely and finely sculptured all over, and I conclude we have only the one variable species.

Genus Onithochiton Gray, 1847
Type species: Chiton undulatus Quoy & Gaimard, 1835 (non Wood, 1828) = Onithochiton neglectus Rochebrune, 1881, New Zealand.
Synonym: Nodiplax Beu, 1967; type species: Icoplax chathamensis Dell, 1960 (= Onithochiton neglectus Rochebrune, 1881).

Girdle with minute pointed scales, appearing like velvet; posterior valve unslit, with mucro at posterior end; second valve longer than the other intermediate valves.

Onithochiton neglectus Rochebrune, 1881 -

The sole species occurring in N.Z., with velvety pink to mauve girdle, valves smooth when adult but coarsely nodulose on many juveniles. Two subspecies can be recognised -

O. neglectus neglectus

Mainland New Zealand, common under intertidal boulders and dredged in shallow water; uniform bright to brownish pink and (in some specimens) coarsely nodulose in juvenile phase (= marmoratus Wissel, 1904, = chathamensis Dell, 1960) but grow up to have a smooth surface and bright, pale, concentric green and cream colour bands on most specimens (a few have some or all valves dark brown).

Shells from under Durvillea holdfasts (=opiniosus Iredale & Hull) are usually perfectly normal O. neglectus neglectus; the holotype of opiniosus is a specimen that has been heavily bored, and so has been distorted in growth to keep up with internal calcification over the borings.

O. neglectus subantarcticus Suter, 1907 -

Subantarctic specimens are all uniform dark brown, but otherwise agree exactly with O. neglectus neglectus; Stewart Island populations include both the dark brown and the pale, banded forms.

Suborder Acanthochitonina
Family Acanthochitonidae Pilsbry, 1893

Five slits in anterior valve, and five radial ribs (if any); lateral and central areas distinguished (if at all) by a radial rib only, bearing some sculpture; sculpture of low, flat, closely spaced nodules in almost all species; girdle with sutural tufts of stiff calcareous spines in all species.

Genus Acanthochitona Gray, 1821
Type species: Chiton fascicularis Linnaeus, 1758, Mediterranean and E.N. Atlantic.

Features as for family; valve area of moderately large size, visible on all species; all with spicules on girdle or, if smooth, with sutural spine tufts.

Subgenus Acanthochitona sensu stricto

Head valve lacking radial ribs; girdle relatively narrow and valves correspondingly large.

Acanthochitona (Acanthochitona) thileniusi (Thiele, 1909) -

Similar to A. zelandica, but with much shorter and thicker calcareous spines on the girdle; known from only a few specimens from Mount Maunganui, Tauranga.

Acanthochitona (Aconthochitona) zelandica (Quoy & Gaimard, 1835) -

A variable species common intertidally throughout New Zealand. Easily recognised by the small, rounded, red or green valves, no radial ribs on the anterior valve, wide smooth girdle, and large tufts of long, blue-green spines at the valve sutures and around end valves. I can see no differences between northern specimens (hookeri Gray) and central N.Z. ones. Some specimens from southern N.Z. are larger than most and have even longer, bright blue-green spine tufts than others (amplificatus Iredale & Hull) but these occur under the same boulders as, and intergrade with, typical A. zelandica. A. brookesi Ashby is based on strongly sculptured variants from Auckland Harbour.

Subgenus Notoplax H. Adams, 1861
Type species: Cryptoplax (Notoplax) speciosa H. Adams, 1861, S.E. Australia.

A highly varied assemblage of many species in N.Z., Australia and Japan. Most have smaller exposed valve areas, correspondingly wider girdles, and smaller spine tufts than in Acanthochitona sensu stricto, but the whole assemblage intergrades with Acanthochitona in almost all features, and the only objective distinction is the presence of five radial ribs on the anterior valve in Notoplax.

Acanthochitona (Notoplax) aupouria (Powell, 1937) -

The single complete, live-taken specimen known to me (National Museum) is from 250 m, off the Three Kings Islands. Quite large (30 mm long, 15 mm wide), with a very wide, deep brownish pink

girdle, felted all over with minute spicules; the spine tufts are small, but situated on raised papillae. Exposed shell areas small, triangular, and separated by areas of girdle, each with a smooth, straight-sided jugum, and lateral areas sculptured with many rows of small, even, closely spaced nodules. Powell (1937) noted that it is more like A. speciosa (S.E. Australia) than any other N.Z. species, and this is confirmed by the wide, spicule-felted girdle of the complete specimen.

Acanthochitona (Notoplax) cuneata (Suter, 1908) -

A very beautiful, pale mauvish pink species, extremely similar to A. violacea in size, proportions, and shape of the valves. The triangular valves are almost smooth, and polished, with only a few shallow, triangular grooves (cuneiform, hence name) on top, as if very large, flat nodules have fused together except for a few small interspaces. Usually thought of as rare, but really just lives in an unusual habitat, crawling along buried under the surface off sand beaches. Abundant at Pilot Bay, Tauranga, and known as far south as Nelson and Wellington Harbour.

Acanthochitona (Notoplax) facilis (Iredale & Hull, 1931) -

A rare, small, very narrow species, with extremely large, coarse nodules all over the shell area. Originally recorded from an Otago intertidal specimen, but hardly known intertidally otherwise; I've seen a few specimens dredged in shallow water all around N.Z. that I'd include here.

Acanthochitona (Notoplax) latalamina (Dell, 1956) -

A large (to about 60 mm long), deep water species with an extremely wide grey girdle, felted all over with large spicules, and with extremely reduced, narrowly triangular shell areas and proportionately huge sutural laminae. Similar to aupouria Powell, but with still smaller shell areas. Known by only a few specimens from Cook Strait and the Chatham Rise.

Acanthochitona (Notoplax) mariae (Webster, 1908) -

The next most common and most widely distributed N.Z. species after A. violacea, occurring all around N.Z., intertidally and down to deep water. The girdle of live specimens is quite wide, finely felted all over with minute spicules, and with small spine tufts. The valves are relatively wide and flat, uniform pink, orange, green or grey, evenly sculptured with small, closely spaced lozenges except for a smooth, narrowly triangular jugum. The wide, shallowly rounded anterior valve has five weak radial ribs. Specimens identified as mariae from deep water off Otago (400 - 500 m) have the same sculpture as intertidal ones, but have more widely triangular juga and very steeply angled backs, and almost intergrade with websteri Powell. The status of deep water ones and websteri are in doubt.

Acanthochitona (Notoplax) rubiginosa (Hutton, 1872) -

A common subtidal species throughout N.Z. Girdle narrow and valves relatively very short and wide, always deep to bright red, head valve with 5 weak to moderately prominent radial ribs, valves sculptured with even, fine nodules all over lateral areas.

Put in Craspedochiton by Iredale & Hull, but Craspedochiton is similar to Loricella and Placiphorella in having the girdle narrow posteriorly but very wide anteriorly, and is limited to tropical species.

Acanthochitona (Notoplax) violacea (Quoy & Gaimard, 1835) -

Our most common Notoplax, large (up to ca. 70 mm) with a wide, smooth, leathery, orange girdle, relatively small but solid and coarsely sculptured orange valves, bright purple jugal areas, and prominent radial ribs on the anterior valve. Under intertidal boulders, all around N.Z., but more common in the north.

Acanthochitona (Notoplax) websteri (Powell, 1937) -

Known by separate valves only, from deep water off the Three Kings Islands; similar to mariae, but with a more widely triangular jugal area. May be a variant of mariae.

Genus Cryptoconchus Burrow, 1815
Type species: Chiton (Cryptoconchus) porosus Burrow, 1815, New Zealand

With extremely wide, smooth, leathery girdle, small spine tufts on raised papillae, and extremely small, narrow, scarcely visible shell areas, but large internal shell plates.

Cryptoconchus porosus (Burrow, 1815) -

Large, up to 100 mm long, common under intertidal boulders throughout N.Z., the well-known "butterfly chiton" with almost no shell visible from the exterior; girdle green, orange, brown or black.

Summary - a list of valid New Zealand chitons

This list has added in the Macquarie Island species traditionally included by Dr Powell (not described above), and includes 3 exclusively Macquarie species, a total of 48 species and subspecies, and 6 unnamed species. Dr Powell ("Shells of N.Z.," 1977 ed.) lists 57 New Zealand and Macquarie species, not counting the 6 unnamed ones listed here, so about 15 names have been deleted from Dr Powell's list.

Family Lepidopleuridae
Genus Lepidopleurus Risso, 1826
(fairchildi (Iredale & Hull, 1929) (probably = L. kerguelensis Haddon, 1866), Macquarie)
finlayi Ashby, 1929
inquinatus (Reeve, 1847)
otagoensis (Iredale & Hull, 1929)
subantarcticus (Iredale & Hull, 1930)
n. spp., Northland

Genus Parachiton Thiele, 1909
textilis Powell, 1937

Family Hanleyidae
Genus Hemiarthrum Dall, 1876
(setulosum Dall, 1876 (= hamiltonorum Iredale & Hull, 1932), Macquarie).
n. gen., n. sp., in Cookia algal crusts.

Family Ischnochitonidae
Genus Ischnochiton Grey, 1847
Subgenus Simplischnochiton van Belle, 1974
circumvallatus (Reeve, 1847)
maorianus Iredale, 1914
(mawsoni Cotton, 1937, Macquarie)

new genus
granulifer (Thiele, 1909) (?subsp. of luteoroseus?)
luteoroseus (Suter, 1907)

Genus Lepidozona Pilsbry, 1892
n. sp.

Family Callochitonidae
Genus Callochiton Gray, 1847
crocinus (Reeve, 1847)
empleurus (Hutton, 1872)

Genus Eudoxochiton Shuttleworth, 1853
nobilis (Gray, 1843)

Family Schizochitonidae
Genus Lorica H. & A. Adams, 1852
haurakiensis Mestayer, 1921

Genus Loricella Pilsbry, 1893
profundior (Dell, 1956)

Family Mopaliidae
Genus Plaxiphora Gray, 1847
Subgenus Plaxiphora sensu stricto
aurata (Spalowsky, 1795)
biramosa (Quoy & Gaimard, 1835)
caelata caelata (Reeve, 1847)
caelata schauinslandi Thiele, 1909
Subgenus Guildingia Pilsbry, 1893
obtecta Pilsbry, 1893
Subgenus Fremblya H. Adams, 1861
egregia (H. Adams, 1861)
Subgenus Vaferichiton Iredale & Hull, 1932
australis (Suter, 1907)
murdochi (Suter, 1905)
n. spp., 2

Genus Placiphorella Dall, 1879
n. sp.

Family Chitonidae
Genus Chiton Linnaeus, 1758
glaucus Gray, 1828
pelliserpentis Quoy & Gaimard, 1835
torri Suter, 1907

Genus Rhyssoplax Thiele, 1893
canaliculata (Quoy & Gaimard, 1835)

Genus Onithochiton Gray, 1847
neglectus neglectus Rochebrune, 1881
neglectus subantarcticus Suter, 1907

Family Acanthochitonidae
Genus Acanthochitona Gray, 1821
Subgenus Acanthochitona sensu stricto
thileniusi (Thiele, 1909)
zelandica (Quoy & Gaimard, 1835)
Subgenus Notoplax H. Adams, 1862
aupouria (Powell, 1937)
cuneata (Suter, 1908)
facilis (Iredale & Hull, 1931)
latalamina (Dell, 1956)
mariae (Webster, 1908)
rubiginosa (Hutton, 1872)
violacea (Quoy & Gaimard, 1835)
websteri (Powell, 1937)

Genus Cryptoconchus Burrow, 1815
porosus (Burrow, 1815)

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Greatly enlarged drawings of New Zealand chitons by R.C. Brazier, N.Z. Geological Survey.

A, B. - Onithochiton neglectus neglectus, head and tail ends of enrolled juvenile specimen (paratype of Icoplax chathamensis Dell).

C, D - Lorica haurakiensis, head and intermediate valves of a fossil specimen.

E. - Rhyssoplax canaliculata, tail valve (fossil).

F. - Parachiton textilis, tail valve (paratype).

G. - Lepidopleurus finlayi, intermediate valve from the holotype.

H. - Lepidopleurus inquinatus, head end.

I. - Lepidopleurus otagoensis, head end.

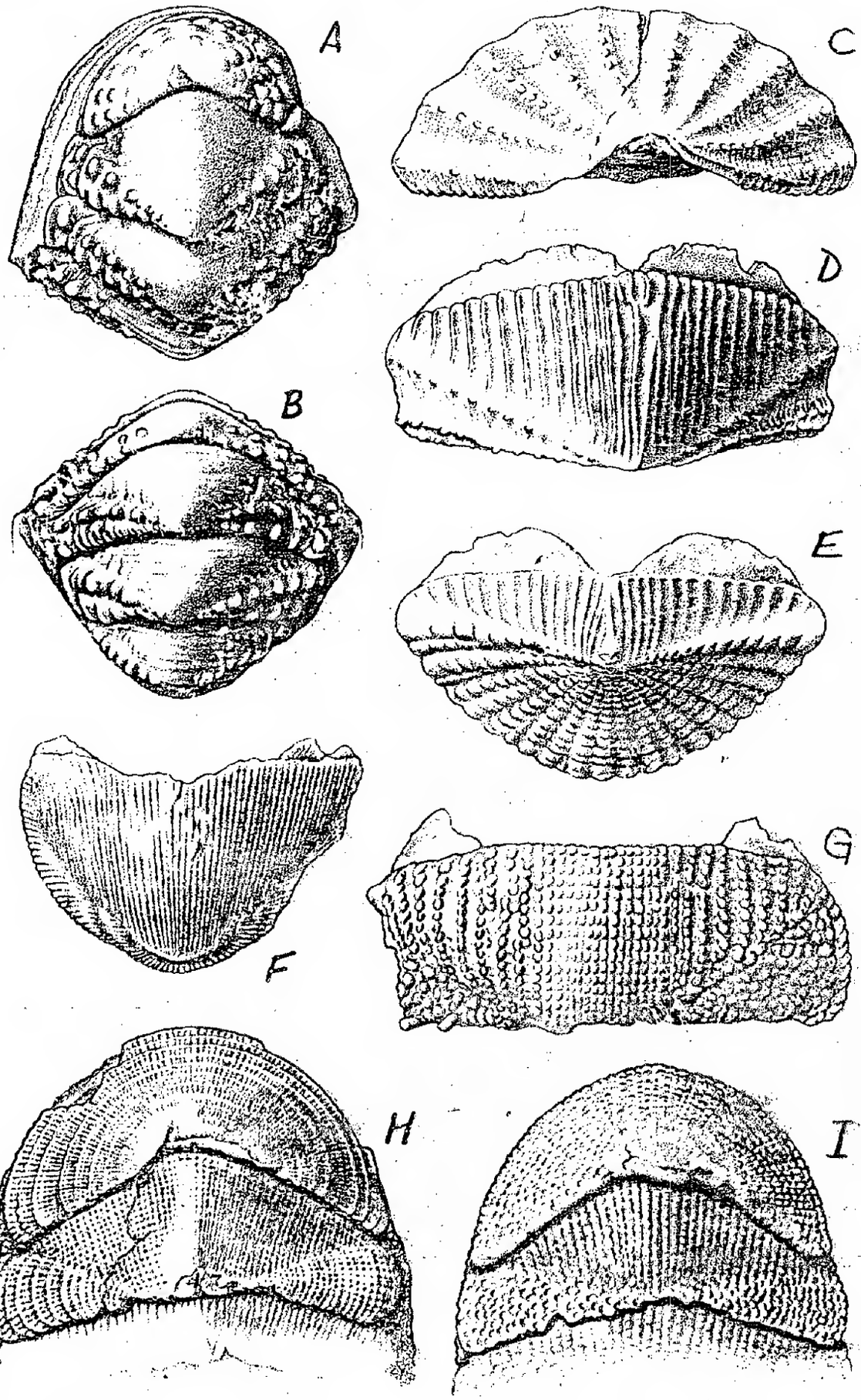
J, K. - Acanthochitona (Notoplax) facilis, head and tail ends of the enrolled holotype.

L,M, N- Acanthochitona (Notoplax) mariae, head, intermediate and tail valves of one specimen.

O. - Acanthochitona (Notoplax) websteri, intermediate valve.

P. - Cryptoconchus porosus, intermediate valve.

Q,R,S.- Acanthochitona (Notoplax) facilis, head, intermediate and tail valves from a Chatham Islands specimen.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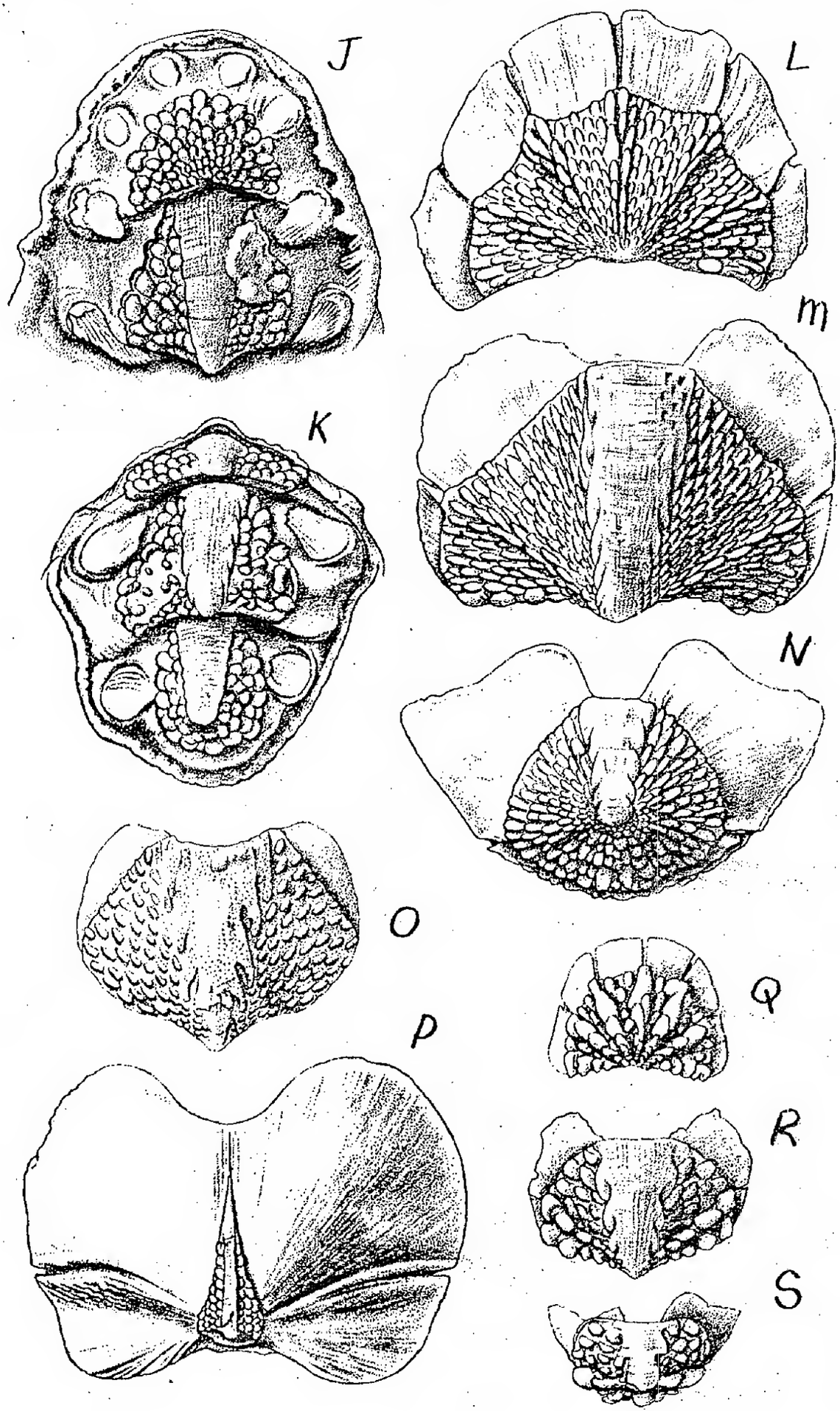
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THE POWELLIPHANTA GILLIESI-TRAVERSI-HOCHSTETTERI-ROSSIANA-LIGNARIA-SUPERBA RING SPECIES (MOLLUSCA: PULMONATA: RHYTIDIDAE)

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ABSTRACT

An alternative classification of Powelliphanta Oconnor, 1945 is presented. Powelliphanta gilliesi (Smith, 1880) and P. hochstetteri (Pfeiffer, 1862) are recognized as species, and the following five subspecies are recognized within the latter: h. hochstetteri (Pfeiffer, 1862); h. superba (Powell, 1930); h. lignaria (Hutton, 1880); h. rossiana (Powell, 1930); h. fiordlandica (Climo, 1971). A model is explained which suggests that all described Powelliphanta species and subspecies are part of a complex ring species which developed as a result of glacial disjunction of colonies of snails in the South Island and by formation of a Cook Strait land bridge during the last Pleistocene glaciation.

INTRODUCTION. Species of Powelliphanta Oconnor have always attracted collectors because of their great variability in colour, size and coiling. Due to the detailed work of Powell (1930; 1932; 1936; 1938; 1946; 1947; 1949) much of this variability has already been analysed. Species, subspecies and forms have been named or recorded, and, thus, collectors have been provided with information on the whereabouts and morphological characteristics of many populations.

It is my contention that this very detailed (and necessary) early work on Powelliphanta became progressively involved with morphological minutae. For example, the evolution of micro-geographical races in the Karamea region have been discussed in great detail (as subspecies) by Powell (1947, p. 202-6). This has meant that the "real" species and subspecies framework (outlined below, and hinted at in the earlier work) has been masked by a plethora of names which have been applied to minor population characteristics. This large list of names has, by its very complexity, been a psychological barrier to the establishment of alternative explanations on the evolution of Powelliphanta in New Zealand. The existing classification, although making sense on a microgeographical scale (with respect to subspecies concepts) breaks down when species parameters are examined. Most species in the existing classification merge clinally with one another, a situation demanding an alternative species framework.

The alternative classification presented below postulates a complex ring species, divisible into two species and five sub-species. The ring has a long southern appendix and the circle between the two species is completed through a broad hybrid zone

in one place. A model of this ring species is presented below (Fig. 2) and a new classification is presented. Steps leading up to the situation illustrated in Fig. 2 are shown diagrammatically in Fig. 1.

THE MODEL

The model depends upon one basic premise - that prior to the late Pleistocene all snails in the North Island were ornamented with a spiral colour pattern, while those in the South Island were either unicoloured or had a predominant radial colour component (Fig. 1). Since the model fits the morphological problem analysed I have assumed that this premise is correct.

During the complex climatic changes of the late Pleistocene, culminating in the last glaciation, Powelliphanta became divided into two morphological forms in the South Island. In the north west snails were unicoloured and large, while in the south they were much smaller and any colour pattern was radially orientated (Fig. 1). This does not imply that all populations in the north or all those in the south were composed of individuals of the same adult size; depending upon local ecological conditions and chance genetic effects there must have been size variation within these basically large northern and smaller southern snails. At the same time in the North Island, to judge from the relative uniformity of shape, size and colour, of specimens there, there has probably always been less restricted gene flow between populations.

During the last glaciation there was a series of migrations of northern spirally-striped stock southwest across Cook Strait (marked 1st, 2nd, and 3rd in Fig. 2). "Migration" as used here means the final crossing to what is now land in the South Island; not necessarily a complete movement of a population across the total expanse of what is now Cook Strait. The waxing and waning of the land bridge population/s impinged upon separate parts of the South Island at three separate times. To judge from the geographical distribution of similar colour forms either side of Cook Strait, the most recent of these migrations or "waves" was the most southern. Populations within these "waves" probably became established on the land bridge area in the triangle between Cape Egmont, Farewell Spit and the Cook Strait narrows. There would have been considerable intermixing of colonies in this area, a situation ideal for the establishment of a centre of colour polymorphism in these spirally coloured snails.

The first of the southwest "waves" probably impinged upon the Cape Farewell area (gilliesi stock). At some intermediate time a further crossing probably resulted in spirally coloured snails colonizing the northern tip of the Pikikiruna Range (hochstetteri stock), considerably further east than the first crossing. The last, most southern and eastern crossing, took place at two closely spaced intervals. One interval resulted in a transfer of snails with light-coloured bases (hochstetteri bicolor; h. consobrina; traversi koputaroa) into the Marlborough Sounds area and shortly after it a second resulted in dark-based snails making the same crossing (h. obscura; traversi florida; t. otakia).

At this stage in the model it is postulated that sea once more filled Cook Strait in the existing post-glacial period. This left remnants of the wide original area of colour polymorphism, which developed on the Cook Strait land bridge, on the Horowhenua coastal plain in the North Island and in three separate areas in the South Island. Since the height of the last glaciation these Powelliphanta colonies dispersed widely during times of favourable ecological conditions (envisaged as wet climatic periods) and became locally extinct during less favourable conditions. The last set of unfavourable conditions killed Powelliphanta in large areas of the North Island where remains are now only found in the subfossil state in caves, leaving the remainder surviving in remnant populations along the main eastern ranges and on Mt Egmont. It is difficult to assess the effect of the introduction of the Polynesian Rat on Powelliphanta in prehistoric times but it may have played a large part in local extinctions (pers. comm. Dr C.A. Fleming).

In the South Island, gilliesi stock (the first crossing of Cook Strait) moved inland and east to overlap and co-exist with the large, unicoloured shells (superba) found in the more central (and higher) parts of this northern region. At the same time small, southern, radially-coloured snails (rossiana-spedeni) moved north, overlapped with superba stock and hybridization occurred. That is, the most northern part of the southern isolate came to overlap the most southern part of the northern isolate and snails of compatible size mated and produced fertile hybrids. A south-western extension of hochstetteri snails (the second Cook Strait crossing) also penetrated this area of mixing, adding a strong spiral colour element to the complex. The timing of this injection of spiral colour into the hybrid zone, relative to the merging of the two South Island isolates, is probably impossible to determine. It was probably inevitable that with three subspecies moving towards one another (all quite variable in minor details of size and colour pattern) that size-compatible stock from three different sources would finally successfully breed. This mixing of lines need not have been direct. It was probably more likely achieved by pure stock crossing with hybrids resulting from the initial pure stock cross. The group of snails known as lignaria subspecies are interpreted here collectively as a wide hybrid zone, with contributing genetic material from superba (large size; unicolour) rossiana-spedeni (small size; radial colour pattern) and hochstetteri (spiral colour pattern and large size in johnstoni and related forms). The only other way to interpret this lignaria complex is to name microgeographical races (as suggested and partly implemented by Powell, 1947), an action which makes naming of the broader geographic categories impossible.

A flat-spired, very widely umbilicate snail became isolated on Resolution Island during the last glaciation and seems best treated as distinct from the rossiana-spedeni group at this stage.

Near the headwaters of the south branch of Pariwhakaoho Stream, draining east from Parapara Peak, north of Takaka, Nelson, there occur four distinct forms of Powelliphanta. In beech forest at relatively low altitude gilliesi-type snails co-exist with hochstetteri-type snails with no interbreeding apparent. In

beech forest immediately below alpine scrub large, golden, superba-type snails occur. In high alpine scrub on Walker Ridge, 1.5km south of Parapara Peak there occur small, radially coloured snails intermediate in character between southern rossiana-type snails and the most brilliantly coloured lignaria hybrid.

The sympatry between hochstetteri-type and gilliesi-type snails is illustrated in Fig. 2. Western migration of the former around the flanks of Parapara Peak has caused geographical (but not habitat) overlap with superba-type snails moving towards the east at a higher altitude. To further complicate the issue, lignaria hybrids with a strong rossiana influence have moved north in the alpine scrub zone to geographically overlap with superba-type snails, though habitat preferences have kept the populations apart so far. This allopatry appears to have broken down in the Mts Muriel and Flanagan area further south in the Tasman Mountains where large superbaXrossiana hybrids occur in the alpine scrub zone. They are intermediate in size between superba mouatae (see below) and the Parapara Peak snails but lack a strong radial colour pattern and dorsal spiral striae.

The Parapara Peak area has been worthy of special mention because recent migrations have caused two species and three subspecies to overlap in the same geographical area, the three latter kept apart only by altitudinal habitat preferences.

It seems that part of the North Island-derived complex of spiral colour forms will interbreed with South Island-derived snails, whereas other parts will not. The situation is probably best interpreted as a ring-species with a hybrid zone completing the circle in two different directions and Cook Strait breaking the circle in the northeast.

The reproductive isolating mechanism preventing interbreeding between, for example, hochstetteri hochstetteri and gilliesi in northwest Nelson (Fig. 2) is probably adult size. From a mechanical point of view copulation is probably impossible; gilliesi being, on average, about half the size of hochstetteri. Though untested, it is also likely that very closely related hochstetteri stock in the Marlborough Sounds (large shells) and on the Horowhenua Plain (small shells) in the North Island will not interbreed for the same reason.

Interbreeding (inferred from the broad hybrid zone) only occurred between the three subspecies of hochstetteri in the Karamea region because snails of compatible adult sizes happened to overlap in the same habitat. Therefore, the one character which maintains the distinctiveness of gilliesi in the South Island in the presence of h. hochstetteri in some localities and h. superba in others, is probably its small size. North Island Horowhenua hochstetteri (traversi in existing checklists) are compatible in size with north-west Nelson gilliesi and the two would possibly interbreed if brought together, since as suggested in the model above their common ancestor lived only 10-20 thousand years ago.

The possibility exists, then, that gilliesi is only a subspecies

of hochstetteri. In that event, not only would Powelliphanta exhibit characteristics of a complex ring species but would otherwise defy easy classification by having reproductively isolated units within subspecies. I do not exclude the latter paradoxical situation, but, at this stage in the presentation of Powelliphanta evolution (an idea to be tested only), do not want to unnecessarily complicate the already complicated two-species model. This refinement of the above basic idea must await the results of breeding experiments, a better understanding of the factors controlling size variability between populations of similarly coloured shells, and more intensive collecting in the central mountainous area of northwest Nelson.

ALTERNATIVE CLASSIFICATION

Genus: Powelliphanta Oconnor, 1945
Type species: Helix hochstetteri Pfeiffer, 1862

I have shown (Climo, 1977, p. 59-65) why Powelliphanta should be regarded as a genus distinct from Paryphanta Albers, 1850. All names relegated to synonymy below would be usefully employed to informally categorize the colour forms of each subspecies. For example, Powelliphanta hochstetteri obscura would be cited Powelliphanta hochstetteri hochstetteri forma obscura.

Powelliphanta hochstetteri (Pfeiffer, 1862)

The species is interpreted here as including all named Powelliphanta with the exception of the gilliesi series. Five subspecies are recognized below. Only the first citation of each named taxon is given in the synonymies.

Powelliphanta hochstetteri hochstetteri (Pfeiffer, 1862)

1862 Helix hochstetteri Pfeiffer, Mal. Bl. 8:146

1901 Paryphanta hochstetteri obscura Beutler, Zool. Jahrbucher, Anat. 14: 369

1930 Paryphanta hochstetteri bicolor Powell, Rec. Auck. Inst. Mus. 1(1):40

1930 Paryphanta traversi Powell, Rec. Auck. Inst. Mus. 1(1):50

1932 Paryphanta marchanti Powell, Rec. Auck. Inst. Mus. 1(3): 158

1936 Paryphanta hochstetteri consobrina Powell, Rec. Auck. Inst. Mus. 2(1): 29

1938 Paryphanta hochstetteri anatokiensis Powell, Rec. Auck. Inst. Mus. 2(3): 133

1938 Paryphanta traversi tararuaensis Powell, Rec. Auck. Inst. Mus. 2(3): 138

1946 Paryphanta traversi florida Powell, Rec. Auck. Inst. Mus. 3(2):120

1946 Paryphanta traversi otakia Powell, Rec. Auck. Inst. Mus. 3(2): 121

1946 Paryphanta traversi koputaroa Powell, Rec. Auck. Inst. Mus. 3(2): 136

1949 Paryphanta traversi latzzona Powell, Rec. Auck. Inst. Mus. 3(6):359

The subspecies is quite characteristically boldly spirally colour-banded. Individual population characteristics have been outlined in detail under the various names listed in the synonymy. P. h. hochstetteri occurs sympatrically with its possible ancestor on Parapara Peak where it seems that reproductively isolated parts of the ring-species overlap.

Powelliphanta hochstetteri superba (Powell, 1930)

1930 Paryphanta superba Powell, Rec. Auck. Inst. Mus. 1(1):41

1936 Paryphanta mouatae Powell, Rec. Auck. Inst. Mus. 2(1): 31

1946 Paryphanta superba prouseorum Powell, Rec. Auck. Inst. Mus. 3(2): 109

1946 Paryphanta superba richardsoni Powell, Rec. Auck. Inst. Mus. 3(2): 110

1946 Paryphanta superba harveyi Powell, Rec. Auck. Inst. Mus. 3(2): 110

This large, chiefly unicoloured northwest Nelson subspecies grades into a more southern complex hybrid zone, listed below, and the arbitrary cut-off point in the old classification is retained; that is, superba mouatae marks the end of subspecies superba and lignaria annectens marks the beginning of the hybrid zone.

Powelliphanta hochstetteri rossiana (Powell, 1930)

1930 Paryphanta rossiana Powell, Rec. Auck.Inst. Mus. 1(1):44

1932 Paryphanta spedeni Powell, Rec. Auck. Inst. Mus. 1(3): 159

1936 Paryphanta rossiana fletcheri Powell, Rec. Auck. Inst. Mus. 2(3): 135

1936 Paryphanta rossiana gagei Powell, Rec. Auck. Inst. Mus. 2(3): 136

1946 Paryphanta spedeni lateumbilicata Powell, Rec. Auck. Inst. Mus. 3(2): 105

1949 Paryphanta rossiana patrickensis Powell, Rec. Auck. Inst. Mus. 3(6): 358

Although constantly small, this subspecies is quite variable in other features. Some populations have spiral striae on the dorsal surface, others are completely smooth, while in yet others the striae are only found on the apical whorls. The degree of shell acceleration is variable. The strength of the radial colour banding is also variable but is most strongly shown in specimens from Wolf River near Milford Sound.

This subspecies grades into the lignaria complex via patrickensis (synonymy above) - and larger shells from the Lower Buller Gorge - into so-called lignaria unicolorata (synonymy below).

The following new colonies are recorded:

1. Upper Lower Buller Gorge, Nelson. P.C. Cresswell. 4/VIII/1975. Map reference: S31 348607

2. Waiatoto Valley, South Westland, T.V. Thompson. -/I/1975

3. Wolf River, just north of Milford Sound. Sea level to 200m. A. Cragg. 15/XII/1976

In view of the broad-category classification presented here I cannot accept that a larger egg size distinguishes spedeni from rossiana - all other features overlap.

Powelliphanta hochstetteri fiordlandica (Climo, 1971)

1971 Paryphanta (Powelliphanta) fiordlandica Climo, Rec. Dom. Mus. Wellington 7(15): 147

A small, widely umbilicate subspecies from Resolution Island with a spirally striate dorsal surface.

Powelliphanta hochstetteri lignaria (Hutton, 1880)

1880 Paryphanta lignaria Hutton, Trans. N.Z. Inst. 20: 43

1930 Paryphanta unicolorata Powell, Rec. Auck. Inst. Mus. 1(1): 43

1936 Paryphanta annectens Powell, Rec. Auck. Inst. Mus. 2(1): 30

1938 Paryphanta lignaria oconnori Powell, Rec. Auck. Inst. Mus. 2(3): 134

1938 Paryphanta unicolorata rotella Powell, Rec. Auck. Inst. Mus. 2(3): 137

1946 Paryphanta lignaria johnstoni Powell, Rec. Auck. Inst. Mus. 3(2):107

1949 Paryphanta lignaria lusca Powell, Rec. Auck. Inst. Mus. 3(6): 350

1949 Paryphanta lignaria ruforadiata Powell, Rec. Auck. Inst. Mus. 3(6): 353

I have named this group of populations with mixed origins as a subspecies for two reasons. Firstly, the hybrid zone is large (as one would expect from the overlap of three subspecies) and quite distinctive as a collective unit of shape and colour varieties. Secondly, and more important, Article 17(2) of the International Code on Zoological Nomenclature states that a name cannot be treated as unavailable just because it can be shown that it is applied to a hybrid. The name lignaria, therefore, has to be formally used somewhere. It cannot, however, be used formally and correctly (in a biological sense) at the same time.

Powelliphanta h. lignaria is not a subspecies in the sense that h. superba, h. hochstetteri, h. fiordlandica or h. rossiana are: it is a hybrid zone caused by the overlap of superba, rossiana and hochstetteri stock. To express this situation formally I am compelled to name the hybrid zone. To do otherwise would be to drop from all formal citation eight names, listed above under lignaria

Powelliphanta gilliesi (Smith, 1880)

1880 Paryphanta gilliesi Smith, Ann. Mag. Nat. Hist. (5) 6: 159

1930 Paryphanta gilliesi subfusca Powell, Rec. Auck. Inst. Mus. 1(1): 47

1930 Paryphanta compta Powell, Rec. Auck. Inst. Mus. 1(1): 48

1930 Paryphanta fallax Powell, Rec. Auck. Inst. Mus. 1(1): 49

1936 Paryphanta gilliesi kahurangica Powell, Rec. Auck. Inst. Mus. 2(1): 33

1936 Paryphanta jamesoni Powell, Rec. Auck. Inst. Mus. 2(1): 35

1938 Paryphanta gilliesi brunnea Powell, Rec. Auck. Inst. Mus. 2(3): 138

1946 Paryphanta gilliesi aurea Powell, Rec. Auck. Inst. Mus. 3(2): 113

The details of variation in this quite variable, small, spirally-coloured snail are given in descriptions of the named forms.

CONCLUDING REMARKS. Powell (1936, p. 29) made the following comment when discussing Simpson's rationale for naming a host of colour varieties of the tree snail Liguus: "He admits that many of the forms he has named are, doubtless, fertile hybrids, but nevertheless they are important in elucidating the story of past development, migration and distribution." By using this argument to justify naming forms of Powelliphanta, and interpreting their evolution, Powell provided the initial ideas and documented nearly all the morphological data which has enabled me to present the above classification. I think I have shown that the evolution of Powelliphanta can be interpreted without retaining all the names but whether this state of affairs could have been reached if the snails had not been named in the first place is doubtful.

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Climo ... Powelliphanta ring species .. explanation of figs.

Fig. 1 Evolution of Powelliphanta showing hypothetical sequence of events leading up to the present complex situation shown in Fig. 2. A, Pliocene Powelliphanta; B, late Pliocene formation of Cook Strait with subsequent evolution of spirally-coloured snails to its north and radially-coloured to the south; C, Pleistocene glacial truncation of South Island colonies resulting in the evolution of fiordlandica stock (black), rossiana stock (vertical lines) and superba stock (white); D, last glaciation and subsequent times, with migration of hochstetteri stock (horizontal lines) across a Cook Strait land bridge and movement of rossiana and superba stocks towards each other. Dotted line represents distribution of land.

Fig. 2 Model showing how the keyed Powelliphanta taxa might have evolved. Arrows indicate snail migrations instrumental in the formation of two species and five subspecies. See text and Fig. 1 for events leading up to situation illustrated here.